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## Subspeciation in the Australian-endemic Great Bowerbird *Chlamydera nuchalis* (Ptilonorhynchidae): a review and revision

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The Great Bowerbird *Chlamydera nuchalis* is an endemic Australian polygynous species. It occurs across tropical northern and north-eastern Australia, from the western Kimberley of Western Australia eastward to the Queensland coast, and thence northward to Cape York on northern-most Cape York Peninsula, and southward in eastern Queensland to areas of the upper Burdekin River/Mackay (Fig. 1). It belongs to the only bowerbird genus adapted to relatively dry, sparsely-vegetated habitats, where it frequents riverine woodlands and vine thickets, eucalypt and melaleuca woodlands, open savannah woodlands and planted suburban areas.

Adult males and females have almost identical plumage, in variable warm greys to brown-greys throughout head, neck and underparts, with upperparts pale (in west and north) to dark (in east) blackish-brown, with extensive broad whitish tipping and edging to all feathers below the nape. Subadult to adult males and a few (? older) females have the upper nape supporting a nuchal crest of erectile silky pink feathers. Immatures and females of some populations show conspicuous ventral barring, particularly on the flanks, which is only faintly discernible on older birds and is absent on adult males. Plumages remain inadequately understood owing to insufficient numbers of specimens from several localities for each named subspecies, sex, age class, month, and because of complicating variation in plumage wear (Mayr & Jennings 1952). For detailed plumage descriptions, and/or illustrations of them, see Mayr & Jennings (1952), Marshall (1954), Gilliard (1969), Cooper & Forshaw (1977) and Donaghey (1996).

To facilitate easier comprehension of subsequent text a summary of more significant Great Bowerbird subspecies descriptions, and brief plumage diagnosis of them (after Gilliard 1969), follows. The

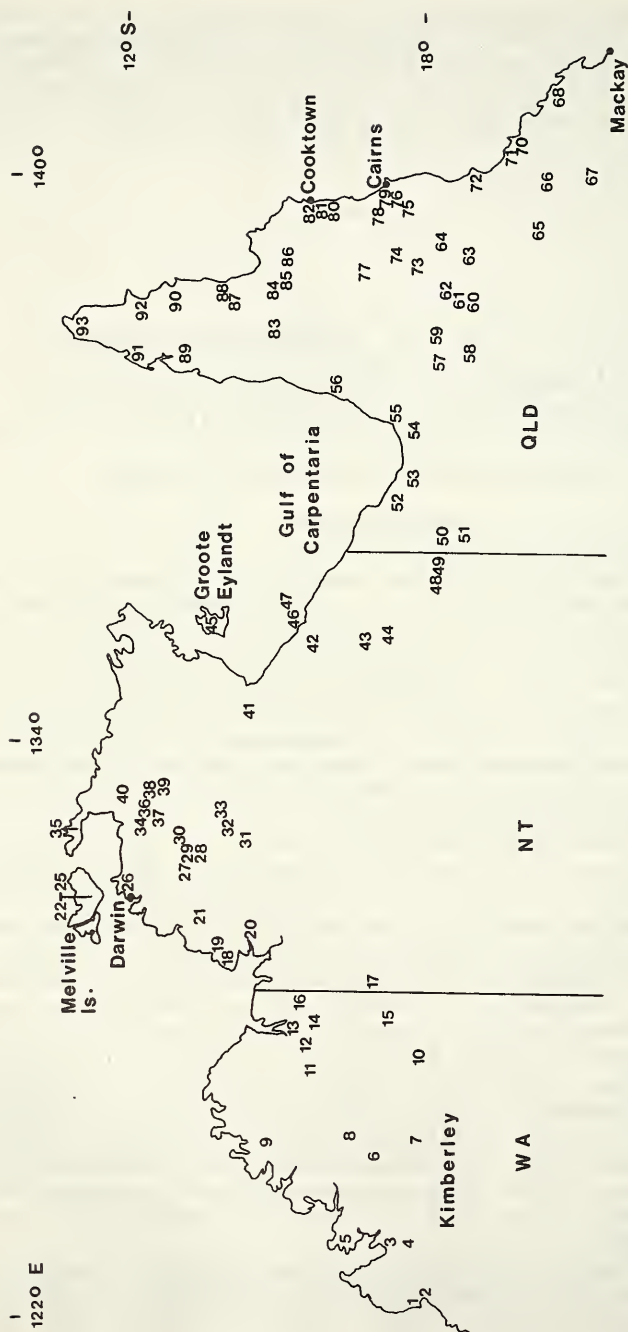


Figure 1. Map of tropical northern Australia with the location of 242 Great Bowerbird skin specimens plotted from west to east. A single specimen is from each location unless a larger number is indicated in parenthesis after the following location numbers: 1 (3), 3(10), 4 (3), 7 (2), 8 (4), 9 (4), 10 (2), 13 (5), 14 (4), 17 (2), 21 (2), 22 (7), 23 (7), 25 (3), 26 (2), 29 (2), 30 (2), 32 (2), 34 (3), 35 (9), 37 (2), 39 (2), 40 (4), 41 (6), 42 (6), 43 (2), 45 (3), 46 (2), 48 (2), 51 (2), 52 (3), 54 (2), 55 (2), 56 (8), 58 (3), 59 (5), 64 (4), 65 (2), 67 (2), 68 (7), 70 (3), 74 (3), 77 (2), 78 (2), 79 (11), 81 (6), 82 (8), 83 (2), 87 (2), 89 (2), 93 (13). Locations 22-25 are on Melville Island and 46-47 on islands of the Sir Edward Pellew Group. WA=Western Australia, NT=Northern Territory, QLD=Queensland. See text.

erroneous transpositions of subspecies characters in Gilliard (1969), as noted by Hall (1974), have been taken into account.

*C. n. oweni* Mathews (1912): described from Point Torment (No. 3 on Fig. 1), western Kimberley, Western Australia. Like *nuchalis* but somewhat larger.

*C. n. melvillensis* Mathews (1912): described from Melville Island, off northern Northern Territory. Differs from *oweni* in being a little smaller and darker dorsally.

*C. n. nuchalis* (Jardine & Selby 1830): described (as *Ptilonorhynchus nuchalis*) from the type locality (as designated by Mayr & Jennings 1952) of Port Darwin, Northern Territory. Upperparts rather uniform and greyish; female generally uniform greyish below like males.

*C. n. orientalis* Gould (1879): described from Port Denison (No. 68 on Fig. 1), Queensland. Very different from *nuchalis* (and *oweni*) in having the upperparts more contrasting in variegated blackish and whitish markings; also females less uniform below, more inclined to barring and thus differing from males.

*C. n. yorki* Mayr & Jennings (1952): described from Utingu (No. 93 on Fig. 1) Cape York. Like *orientalis* but smaller and generally lighter in all plumages, particularly ventrally.

Rothschild (1898) considered *orientalis* invalid, even at the subspecies level. Mathews (1912) subsumed *C. n. orientalis* into the nominate subspecies, named *C. n. oweni* for the Kimberley birds and erected *C. n. melvillensis* for birds on Melville Island. Later he (Mathews 1930) adopted a similar scheme but merged his *melvillensis* into *C. n. oweni*. Hartert (1929) accepted *oweni* as having larger wings (186–193) than similarly plumaged *nuchalis* (173–186 mm).

Although ambiguously stated, Iredale (1950: 217) acknowledged the four subspecies *oweni*, *nuchalis*, *orientalis* and *yorki*. These were also accepted in the influential review of variation in Australian bowerbirds of Mayr & Jennings (1952) who, while conceding Mathews' characters for *melvillensis* as discernible, rejected this subspecies as "there is little difference between specimens from Melville Island and those from the mainland of Northern Territory, except that the latter average slightly larger." They concluded that geographic variation in the Great Bowerbird is "essentially clinal except for a 'step' between an eastern and western group, at the head of the Gulf of Carpentaria".

Marshall (1954: 90) and Keast (1961) followed Mayr & Jennings (1952) but noted that the subspecies are not "separated to anything like the extent exhibited by the eastern and western populations of the Spotted Bower-bird [*C. maculata*]". Mayr (1962) retained these four subspecies. Deignan (1964) considered Groote Eylandt and mainland Northern Territory birds to be *C. n. melvillensis*. Gilliard (1969) also accepted the subspecies *oweni*, *nuchalis*, *orientalis* and *yorki* and his treatment has been widely followed (e.g. Hall 1974, Cooper & Forshaw 1977, Blakers *et al.* 1984, Donaghey 1996). The few exceptions to this rule are noteworthy and are as follows: Storr (1973, 1984) acknowledged only nominate *nuchalis* and *orientalis* (*yorki*) in

Queensland. Ford (1974, 1987) accepted only *C. n. nuchalis* and *C. n. orientalis* for the species as a whole without discussion. Likewise, Storr (1977, 1980) did not mention *oweni* and treated all birds across the Kimberley and the Northern Territory as nominate *nuchalis*—a treatment also used by Storr *et al.* (1975), Smith *et al.* (1978) and Johnstone & Smith (1981).

There is thus no generally accepted subspecific taxonomy in *C. nuchalis*. Moreover, many authorities consider that, their own taxonomic usage notwithstanding, the apparently contiguous distribution of the species' populations, clinal nature of variation across it, and the weakly-differentiated nature of subspecies leave doubt about the validity of systematic recognition of intraspecific variation. Most recent authors have, however, retained *oweni*, *nuchalis*, *orientalis* and *yorki*, stating that these are weakly differentiated and/or that they clearly form a western subgroup consisting of the former two and an eastern subgroup consisting of the latter two forms. While not attempting to demonstrate or discuss this, a minority of recent authors apparently take this repeated observation as justification to reject *oweni* and *yorki* and thus accept only *nuchalis* in the west and *orientalis* in the east. Because of this we use below "western populations" for *oweni-nuchalis* combined and "eastern populations" for *orientalis-yorki* combined. The purpose of this study is to review and resolve the conflicts and doubts outlined above, to present evidence for and discussion of presently unsubstantiated opinion, and to offer our own conclusions in the light of the results of our examining considerably larger samples than previously studied.

## Methods

We examined all sexed specimens from all recorded localities at or from (on loan to us) the following institutions: Queensland Museum, Brisbane; Australian National Wildlife collection, CSIRO, Canberra; Australian Museum, Sydney; Museum of Victoria, Melbourne; South Australian Museum, Adelaide; Western Australian Museum, Perth; American Museum of Natural History, New York; The Natural History Museum, Tring; National Museums & Galleries on Merseyside, Liverpool; Nationaal Natuurhistorisch Museum, Leiden; Staatliches Museum für Tierkunde, Dresden; Zoologische Staatssammlung, München; Museum Alexander Koenig, Staatliches Museum für Naturkunde, Stuttgart; Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt.

Measurements were taken by CBF: wing length is the flattened and straightened chord along a stopped ruler. Tail length is the maximum length of the longest tail feather from its point of entry into the skin to its tip, measured with an unstopped steel ruler. Other measurements were taken with electronic digital vernier calipers to the nearest whole decimal point. Bill length is that from the union of the bill with the foreshell to the tip of the upper mandible. Tarsus length is that from the intertarsus joint to the lower edge of the last undivided scute before the toes diverge. Where possible, all measurements were taken from

each of 242 museum skins. Differences in mean values of wing and tail measurements between various subspecies combinations were tested for levels of statistical significance by Student's two-tailed *t*-tests.

The 242 museum specimens were taken from 92 different localities across tropical Australia. These were allocated locality numbers 1–93 for the purpose of plotting them on a map predominantly west to east, in numerically ascending order (Fig. 1 which lacks No. 69). For our analysis of biometrics of subspecies groupings we first delimited the distribution of each according to plumage morphology and body size (wing and tail lengths).

Our larger sample notwithstanding, we appreciate that we are dealing with five (including *melvillensis*) named subspecies over a geographically extensive area. This, combined with inadequately understood plumages and complicated by variable plumage wear and unreliable sexing of earlier specimens (Hall 1974; Mayr & Jennings 1952; pers obs.), means that samples of each sex and age group for individual subspecies are inadequate. As a result, we do not separate the sexes or attempt to do so for age or for subgroupings based on relative plumage wear, but use the resultant large samples to derive means for measurements of entire geographic populations. As sexual size dimorphism in the species is but *c.* 4% (e.g. in the enlarged subspecies *C. n. nuchalis* accepted herein, 51 female wing lengths average  $173 \pm 6.98$  SD mm and those of 85 males  $180 \pm 6.58$  mm) this is not unreasonable.

To assess subspecies we compare the biometrics of all discussed taxa separately, and those of various combinations of named populations that constitute subspecies various workers consider valid.

## Results

Of the 242 specimens, 84 were sexed as female. Among these, four birds had only 4–10 individual pink crest feathers present, two had a quarter-developed crest, 3 a third-, 1 a half-, and another a three-quarter-developed crest. We found no females with a fully developed nuchal crest.

Plotting of specimen locations resulted in subspecies distributions of localities 1–17 for *oweni*; 18–21 and 26–53 for *nuchalis* (birds from 16, 18, 21, 27 and 29 exhibited some characters intermediate between those of *oweni* and *nuchalis*); 22–25 for *melvillensis*; 52, 53, 54 for birds intermediate between *nuchalis* and *orientalis*; 55–76 for *orientalis*; 77–82 for birds intermediate between *orientalis* and *yorki*; and 83–93 for *yorki* (see text below and Fig. 1).

### *Variation within the western populations*

The colouration and markings of birds of the east Kimberley are broadly intermediate between birds of the west Kimberley and those of Melville Island. Mathews (1912) correctly observed that Melville Island birds are dorsally darker and are smaller than typical *oweni* but, as Mayr & Jennings (1952) pointed out, these differ very little from *nuchalis* of the immediately adjacent Northern Territory mainland,

other than being slightly smaller (Table 1). This difference in size is not statistically significant for wing length ( $t_{86}=1.33$ ,  $p>0.1$ ) but is significant for tail length ( $t_{85}=3.88$ ,  $p<0.001$ ). We concur with Mayr & Jennings (1952), Mayr (1962) and Gilliard (1969) in considering *melvillensis* a synonym of *nuchalis*.

The distributions of *oweni* and *nuchalis* are contiguous (Blakers *et al.* 1984) but as we found there exists coincidentally a geographically significant gap in the distribution of collected specimens (between localities 17 and 18), immediately to the east of the Western Australia/Northern Territory border (*c.* 129° 30'E—see Fig. 1), we use this in separating them for biometrical comparisons (Table 1). As several authors have done, we noted that one or two specimens from some localities (16, 18, 21, 27 & 29; Fig. 1) of eastern-most *oweni* and western-most *nuchalis* exhibit some plumage characters intermediate between the typical plumages of the two forms.

With *melvillensis* subsumed into *nuchalis*, the biometrics for birds of this taxon show *nuchalis* to average 5% smaller in wing and 7% smaller in tail length than *oweni* (Table 2). These differences are statistically significant (wing,  $t_{132}=7.04$ ,  $p<0.001$ ; tail,  $t_{131}=9.95$ ,  $p<0.001$ ). This should, however, be seen as part of a conspicuous cline in average size across the Australian tropics from larger western birds to smaller eastern ones (see Table 1, Fig. 2), particularly in view of the similar plumage in *oweni* and *nuchalis* (including *melvillensis*).

#### *Variation within the eastern populations*

The dorsal colouration and markings of *orientalis* and *yorki* are, as described by Mayr & Jennings (1952), darker and thus more variegated or contrasting in pattern, and the ventral plumage, particularly the flanks, more usually and strongly barred than in the western populations (*oweni* and *nuchalis*). As also noted by Mayr & Jennings, *yorki* average slightly paler, more so ventrally and particularly on the throat, and smaller than *orientalis* (Table 1). The differences in plumage colouration and pattern are slight but size differences are statistically significant in lengths of both wing ( $t_{76}=7.61$ ,  $p<0.001$ ) and tail ( $t_{76}=7.64$ ,  $p<0.001$ ). Excluding the intermediate individuals from the three Cooktown area localities (see above), typical *yorki* individuals average 5% smaller in wing length and 4% in tail length than *orientalis*. Despite the statistical significance, differences in size are no more than part of the conspicuous cline in size mentioned above (see Table 1 and Fig. 2).

The distributions of *orientalis* and *yorki* are contiguous (Blakers *et al.* 1984) but there exists a geographical gap in the distribution of specimens (locality 56 excepted) immediately to the south of Cooktown (between localities 77–79 and 80, at *c.* 16°00'S—see Fig. 1), which we use in separating them for biometrical comparisons (Table 1). We noted, like Mayr & Jennings (1952), that one or two specimens from some localities of northern-most *orientalis* and southern-most *yorki* exhibit some plumage characters intermediate between typical plumage of the two forms; the localities involved are 77 to 82, and particularly 80–82 (Fig. 1). Likewise, the few specimens from the head of the Gulf

TABLE 1  
Measurements of specimens of subspecies, some subspecies combinations, and some intermediate specimens of the Great Bowerbird  
*Chlamydera nuchalis*

	<i>oroni</i>	<i>melvillensis</i>	<i>nuchalis</i>	<i>nuchalis</i> plus <i>melvillensis</i>	<i>orientalis</i>	<i>intermediate</i> <i>orientalis</i> - <i>yorki</i>	<i>yorki</i>
Mean wing length (n)	183 (46)	173 (18)	175 (70)	174 (88)	175 (52)	169 (30)	166 (26)
SD	6.0	5.3	7.0	6.7	5.4	5.3	6.4
range	171-196	164-182	158-189	158-189	162-186	158-179	155-179
Mean tail length (n)	152 (46)	137 (18)	143 (69)	141 (87)	134 (52)	133 (30)	128 (26)
SD	6.1	5.9	5.6	6.0	5.2	5.2	6.3
range	140-165	127-146	133-158	127-158	123-149	123-144	121-143
Mean tail/wing ratio (%)	83	79	82	81	77	79	77
Mean tarsus length (n)	48.7 (46)	47.4 (18)	47.3 (70)	47.3 (88)	46.4 (52)	45.3 (30)	45.2 (26)
SD	2.6	2.5	2.2	2.3	2.1	2.0	2.6
range	42.3-54.6	43.2-51.8	42.6-51.1	42.6-51.8	41.0-50.7	40.7-48.7	41.0-52.6
Mean tarsus/wing ratio (%)	27	27	27	27	27	27	27
Mean bill length (n)	38.8 (46)	38.1 (16)	38.3 (66)	38.3 (82)	37.8 (52)	36.8 (30)	38.1 (25)
SD	1.3	1.4	1.7	1.6	1.6	1.6	1.5
range	35.7-41.1	34.5-40.7	32.2-41.6	32.2-41.6	33.7-41.7	32.6-39.7	35.5-41.4
Mean bill/wing ratio (%)	21	22	22	22	22	22	23

TABLE 2

Measurements of specimens of the subspecies *nuchalis* (*oweni*, *melvillensis*) and *orientalis* (*yorki*) of the Great Bowerbird *Chlamydera nuchalis*

	<i>nuchalis</i> ( <i>oweni</i> , <i>melvillensis</i> )	<i>orientalis</i> ( <i>yorki</i> )
Mean wing length (n)	177 (134)	171 (108)
SD	7.6	6.6
range	158–196	155–186
Mean tail length (n)	145 (133)	132 (108)
SD	7.8	6.0
range	127–165	121–149
Mean tail/wing ratio (%)	82	77
Mean tarsus length (n)	47.8 (134)	45.8 (108)
SD	2.5	2.3
range	42.3–54.6	40.7–52.6
Mean tarsus/wing ratio (%)	27	27
Mean bill length (n)	38.5 (128)	37.6 (107)
SD	1.5	1.7
range	32.2–41.6	32.6–41.7
Mean bill/wing ratio (%)	22	22

of Carpentaria, (localities 52, 53, 54; Fig. 1), at the eastern extremity of the range of *nuchalis* and the western extremity of *orientalis*, exhibit some plumage characters intermediate between the typical plumages of these forms, as noted by Hall (1974).

#### *Variation between the western and the eastern populations*

We agree with Mayr & Jennings (1952), Gilliard (1969), and Hall (1974) that the two eastern subspecies share the plumage characters of darker and more brownish upperpart markings, contrasting more with the whitish tips, and with underparts typically less dark. Immature birds show distinct ventral barring, mostly on the flanks, while adults may show no barring at all. Equally significant in our view (see Discussion) is the fact that adult eastern birds (those of westernmost localities 58 and 59 excepted) typically, but not invariably, exhibit the conspicuous feature of extensive silky silvery-white feather tipping, or spotting, on at least the forecrown if not throughout the crown as well as bordering the pink crest in those birds so adorned.

Differences in average wing length between western *nuchalis* and eastern *orientalis* (*sensu stricta*) are not statistically significant ( $t_{120}=0$ ,  $p>0.1$ ) but in tail length are significant ( $t_{119}=9.10$ ,  $p<0.001$ ). This is part of a larger western to smaller eastern birds cline in overall size but not in body proportions (Tables 1 & 2; Fig. 2).

Differences in plumage and size (statistical significance notwithstanding) between the two western subspecies and between the two eastern ones are trivial. By comparison, the paler and less contrasting upperpart markings and uniform crown colour of adults in western populations, as opposed to the darker and more contrasting upperpart markings and the silvery-white feather tipping, or spotting, on the

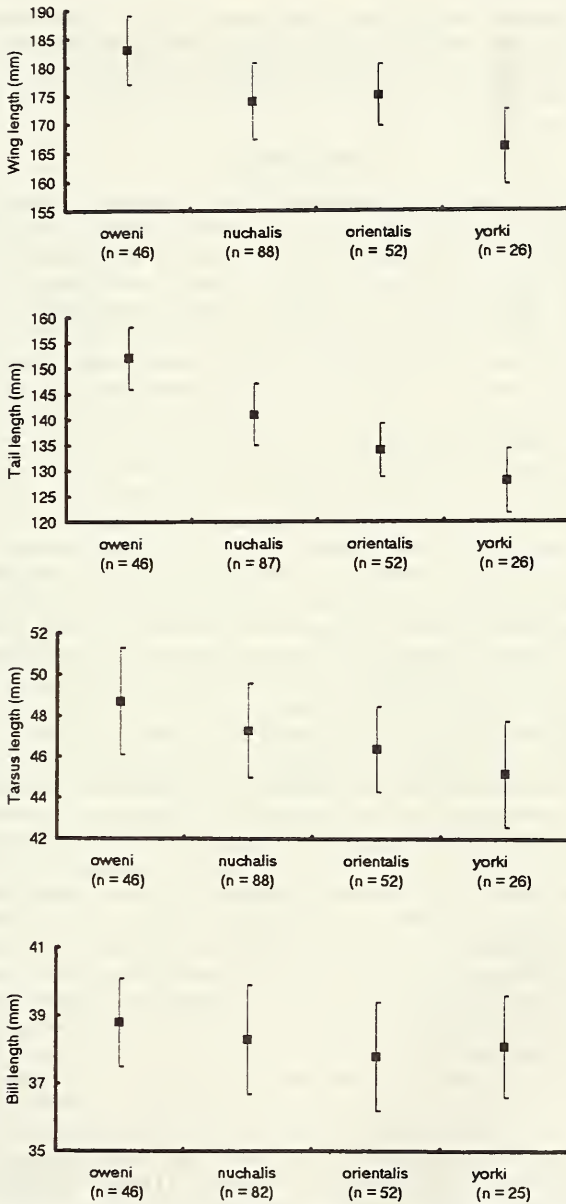


Figure 2. Mean measurements of Great Bowerbird subspecies *oweni*, *nuchalis*, *orientalis* and *yorki* plotted west to east and thence south to north as they are geographically distributed (see Figure 1) to show fundamental west to east cline in decreasing size. Vertical bars show standard deviations and samples sizes are indicated beneath each taxon. See text.

crown in eastern populations, are not trivial. Differences in size between enlarged *nuchalis* (including *oweni* and *melvillensis*) and *orientalis* (including *yorki*) adopted below are significant in both wing ( $t_{240}=7.40$ ,  $p<0.001$ ) and tail ( $t_{239}=14.62$ ,  $p<0.001$ ) length.

## Discussion

Few land bird species distributed over both the Kimberley and Northern Territory are presently considered to show variation worthy of subspecific status between these two areas (e.g. *oweni* and *nuchalis*). Of the potential *c.* 170 species that occur there (Storr 1977, 1980; Blakers *et al.* 1984), only four possible exceptions might be considered: the Partridge Pigeon *Geophaps smithii*, Sandstone Thrush *Colluricincla woodwardi*, Long-tailed Finch *Poephila acuticauda* and the Grey Butcherbird *Cracticus torquatus*. Most authorities do not, however, acknowledge the weakly-differentiated variation between these populations as justifying subspecies rank. Only the Black Grasswren *Amytornis housei*, of the Kimberley, and the White-throated Grasswren *A. woodwardi*, of Arnhemland, have differentiated into species within the Kimberley-Northern Territory area. These species are, however, terrestrial, sedentary inhabitants of limited and isolated areas of specialized habitat. Intraspecific variation in birds between areas of tropical Queensland, north and south of the Cairns-to-Cooktown area, is more commonly acknowledged by subspecific status. This area of tropical Queensland includes, however, greater climatic and habitat diversity (Frith & Frith 1996) than the relatively uniform biota of the Kimberley-Northern Territory area.

Recent authors (Mayr & Jennings 1952, Marshall 1954, Keast 1961, Gilliard 1969, Schodde & Tiedemann 1988) have cited the weakly-defined *C. nuchalis* subspecies, particularly within western and eastern populations, noting that plumage and size variation between them is basically clinal with geographically intermediate populations exhibiting intermediate morphology. Plotting locations of museum specimens demonstrates that few have been collected from areas intermediate between described subspecies, notwithstanding the species' presence in these areas (Blakers *et al.* 1984). Although there are statistically significant differences in sizes of some populations, the west-east cline in size is clear (Table 1 & Fig. 2). Moreover, larger numbers of specimens from the relatively great areas of habitat between subspecies might prove that apparent differences in size between these subspecies are artefacts of insufficient specimen collecting. In plumage, however, any perceived cline is clearly broken by the marked differences in dorsal plumage of adult birds between western *nuchalis* and eastern *orientalis*.

No one but Deignan (1964) has suggested resurrecting Mathew's (1912) *melvillensis* since Mathews himself (1930) subsumed it into *nuchalis*. However, the plumage of Melville Island birds is more diagnostically definable from that of mainland Northern Territory birds (*nuchalis*) than are plumage differences between *oweni* and *nuchalis*. Moreover, the difference in average lengths of wing and tail between *melvillensis* and *nuchalis* are no more or no less significant than

those between *nuchalis* and *orientalis*. Thus if the four subspecies *oweni*, *nuchalis*, *orientalis* and *yorki* are acceptable, as by most authors, it is inconsistent not to accept *melvillensis*.

We agree with Mayr & Jennings (1952), Gilliard (1969) and Hall (1974) that the two western subspecies share the broad plumage characters of paler and less contrasting, more uniform and greyish upperparts and the underparts usually darker. Immature birds exhibit slight and faint ventral (mostly flank) barring (but stronger in some western *nuchalis* than in *oweni*), but adults less so or not at all. As significant, in our view (see above), is that adult western birds typically lack silky silvery-white feather tipping, or spotting, throughout the crown, (showing such feather tipping only immediately about pink nuchal crest feathers when present). Exceptions to this are the birds from the Gulf of Carpentaria (localities 54 and 55, see Fig. 1) that have a little silver tipping on the crown.

Variation in colouration and pattern of the crown between bowerbird populations feature most conspicuously as species and/or subspecies characters, particular in *Ailuroedus*, *Amblyornis* and *Chlamydera* (Gilliard 1969, Frith & Frith 1995, 1997a,b, 1998). While the subspecies of *C. nuchalis* most widely accepted are weakly differentiated because of the fundamentally clinal nature of variation in plumage and size, we find the marked difference in crown morphology between western *nuchalis* and eastern *orientalis* (as defined here) highly significant in combination with the equally marked difference in dorsal plumage colouration and pattern between them. We therefore conclude that only two subspecies should be recognised: *C. nuchalis* in Western Australia and the Northern Territory to the Gulf of Carpentaria in Western Queensland, and *C. n. orientalis* in the east and north-east of Australia. This treatment was repeatedly used by Storr (1967, 1973, 1977, 1980, 1984), Ford (1974, 1987) and by Schodde & Tidemann (1988). These two subspecies meet in the area of the head of the Gulf of Carpentaria, where the few specimens collected show some characters intermediate between them.

The acceptance of only two subspecies, *nuchalis* and *orientalis*, as reflecting variation within *C. nuchalis* accords well with the repeatedly expressed doubts about weak differences within the western and eastern populations and gives appropriate taxonomic weight to the far more obvious morphological "step" between these populations noted by Mayr & Jennings (1952) and reiterated by Gilliard (1969) and Hall (1974).

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## *Mirafra erythrocephala* Salvadori & Giglioli, 1885, an older name for *Mirafra assamica* *marionae* Baker, 1915

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While examining the zoological writings by Enrico Hillyer Giglioli (1845-1909), we discovered that the taxon *Mirafra erythrocephala* Salvadori & Giglioli, 1885, from Cochinchina, posed an identification problem.

This name is not mentioned by J. L. Peters (in: Mayr & Greenway 1960), while Sharpe (1890) dismissed it as a synonym of *Mirafra assamica*, adding the note "pt. hiem." (=winter plumage). The last mention of *M. erythrocephala* as a valid species was by Salvadori (1915). In the same year, Baker (1915) described *Mirafra assamica marionae* from Ayuthia, Central Thailand. This latter name was also employed by Delacour & Jabouille (1931) for the subspecies of *M. assamica* inhabiting French Indochina.

*Mirrafra* [sic!] *erythrocephala* was used again by Arrigoni degli Oddi (1924), listing the new taxa named by T. Salvadori; in 1986 *M.*